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S15-3 Fitness consequences of cooperative breeding in the Seychelles warbler

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Abstract Inclusive fitness benefits have been suggested as the selective force behind the evolution of cooperative breeding. Assessing the benefits accrued to individual males and females is crucial to understanding the sex-specific helping behavior observed in many cooperatively breeding species. We investigated the fitness consequences of male and female helping behavior in the Seychelles warbler (*Acrocephalus sechellensis*). Until 1988, the entire world population of Seychelles warblers was confined to Cousin Island (29 ha), where the carrying capacity has been maintained since 1973. Due to intense competition for breeding vacancies, many young become subordinates within a territory and often help by provisioning non-descendent offspring. On high-quality territories, the benefits accrued by subordinates are higher for females than males. Female subordinates remain on their natal territory and obtain higher inclusive reproductive success by helping closely related relatives, by co-breeding within the group, and through experience in parenting. Males often become subordinates on non-natal territories and so do not gain indirect reproductive success by helping. They only rarely gain direct benefits through co-breeding, and do not gain through the eventual inheritance of the territory. The disparity in the benefits gained by each sex may explain why the majority of subordinates are female. It should be kept in mind that the benefits of cooperation may be later offset by competition between same-sex offspring, and that the balance between these forces determines the reproductive value of sons and daughters.

Key words Seychelles warbler, Cooperative breeding, Fitness benefits, Competition, Territory inheritance, Co-breeding

1 Introduction

Evolutionary theory is based on the concept that individuals are selected on their efficiency in translating resources into reproductive success, thereby maximizing their genetic contribution to future generations (Hamilton, 1964; Maynard Smith, 1964). The fitness of an individual is expected to be affected by the decision to disperse or not (Kokko and Sutherland, 1998; Pen and Weissing, 2000a) and, in cooperatively breeding species, by the decision to help or not (Emlen, 1991; Koenig et al., 1992). If helping results in higher fitness than dispersal, individuals should delay dispersal and help. The most common form of cooperative breeding involves a breeding pair that is assisted by offspring from previous broods. Normally juveniles of one sex are more likely to stay and assist with parental care, while the other is more likely to disperse (reviewed in Stacey and Koenig, 1990; Cockburn, 1998).

To test the fitness benefits of delayed dispersal and helping in the field, detailed knowledge of the fitness functions for males and females is required (Leimar, 1996; Lessells, 1998; Lessells et al., 1998; Koenig and Walters, 1999; Pen and Weissing, 2000b). Such data are not available for most species because of several hurdles. First, dispersal is hard to measure because individuals often leave

the study population. Secondly, measuring reproductive output is complicated because individuals may produce young outside the pair bond (reviewed in Birkhead and Møller, 1992), and because complex patterns of cooperative breeding, ranging from non-breeding to shared reproduction with others, also occur (reviewed in Vehrencamp, 2000). In this paper we review the sex-specific fitness benefits of cooperative breeding in the Seychelles warbler (*Acrocephalus sechellensis*). To our knowledge, asymmetry in sex-specific fitness benefits from cooperative breeding has not been properly assessed before.

The Seychelles warbler is an insectivorous bird endemic to the Seychelles islands in the western Indian Ocean. Although warblers can breed independently in their first year, a lack of suitable independent breeding opportunities drives some individuals to become subordinates within a territory (Komdeur, 1992). The Seychelles warbler is an excellent model species to test the sex-specific fitness benefits of helping behavior because of: (i) the presence of female-specific helping (Komdeur, 1996a; Richardson et al., 2002) and male-specific dispersal (Komdeur, 1992), (ii) the ability to measure local dispersal in detail (Komdeur 1992, 2003), (iii) the availability of molecular markers to assess sex, parentage and coefficients of relatedness between in-

dividuals in the breeding group (Richardson et al., 2000, 2001), and (iv) the wealth of long-term data allowing accurate fitness measures for each individual (Komdeur, 2003). The majority of subordinates occur on high-quality territories, so for simplicity sake and to avoid the possible confounding effects of territory quality, we here consider the benefits gained by male and female offspring in high-quality territories only.

2 Materials and methods

2.1 Study populations and data collection

The Cousin Island population of Seychelles warblers (c. 320 birds) has been intensively studied since 1985, while the populations on the islands of Aride (68 ha) and Cousine (26 ha), established in 1988 and 1990 respectively (Komdeur, 1997), have been studied from establishment. From 1985, nearly all birds on Cousin Island have been banded for individual recognition and, since 1993, blood sampled for molecular sex and parentage analyses. Off-island migration by warblers is negligible (0.13%; J. Komdeur et al., unpublished), so birds that have disappeared are considered dead. In each year of the study period, nearly all breeding attempts were monitored and activity by resident birds observed during the nest building, incubation and nestling periods (Komdeur, 1996b; Richardson et al., 2002).

Observations on incubation and food provisioning were made at all breeding attempts to determine the status of the birds within each territory. The primary male and female were defined as the dominant, pair-bonded male and female in the territory, while the term 'subordinate' included all other resident birds over eight months old in the territory. Subordinates were split into three categories: non-helpers, subordinate helpers (non-parents) and subordinate parents. Playing recorded songs at different locations to provoke territorial defence behavior by the focal birds identified territory boundaries. Territory size was assessed using a compass and aerial photographs. Because the warblers are insectivorous, territory quality was expressed in terms of insect prey availability (Komdeur, 1992), a factor that has been assessed on a monthly basis within each breeding season. Territories were classified into three quality categories: low, medium and high (Komdeur, 1992).

To test whether helping by males results in inheritance of the territory, nine territories that contained a breeding pair and a male helper were selected. For each territory, the primary male was removed and translocated to either Aride in September 1988 ($n = 4$) or Cousine in 1990 ($n = 5$) (Komdeur, 1994a). After the removal of the primary male, focal helpers were kept under daily observation until the breeding vacancy was filled.

2.2 Molecular analyses

The sex of each individual within the study populations was determined using a PCR-based genotyping method (Griffiths et al., 1998). Genotypes were identified for individuals in the Cousin population using 14 microsatellite

markers (Richardson et al., 2000). Coefficients of relatedness between individuals were determined using KINSHIP (Goodnight and Queller, 1999) and employed to determine, in terms of genetic equivalents, the exact direct and indirect benefits gained by subordinates (Richardson et al., 2002). Using CERVUS (Marshall et al., 1998), parentage was assigned with high confidence ($>90\%$) to all offspring sampled between 1997 and 2000 (Richardson et al., 2001).

3 Results

3.1 Benefits of helping: difference between the sexes

In the Seychelles warbler, removal experiments showed that, on high-quality territories, the helping behavior of subordinates increased the reproductive success of focal breeding pairs (Komdeur, 1994a). Furthermore, subordinates were more likely both to become helpers and provide more help when they were closely related to the recipient (Komdeur, 1994b). In this study, however, relatedness was estimated from pedigree data which was shown to be inadequate when, a decade later, we found from microsatellite-based genotyping that complex patterns of shared reproduction and/or extra-group paternity occur in the Seychelles warbler (Richardson et al., 2001, 2002).

It was also found that females always become subordinates on their natal territory ($n = 43$), whereas a significant percentage of males (25%, $n = 20$) became subordinates on non-natal territories ($\chi^2 = 8.51$, $P < 0.05$; Richardson et al., 2002). This suggests that the indirect benefits of helping are more important for females than for males. Using microsatellite markers to calculate precise coefficients of genetic relatedness among individuals (Richardson et al., 2000), we found that female subordinates without parentage accurately maximized indirect benefits by preferentially feeding more related offspring, produced by relatives of the female subordinate. On the other hand, the amount of help provided by male subordinates was low and independent of relatedness to offspring (Richardson et al., 2003).

In the Seychelles warbler, unrelated subordinates (born in other groups) do sometimes help (D.S. Richardson, pers. comm.) It suggests that direct benefits, such as improved parental skills or gaining parentage (Koenig et al., 1992; Cockburn, 1998), or territory inheritance (Emlen, 1991; Koenig et al., 1992; Balshine-Earn et al., 1998), are important too. To test whether helping improved the reproductive success of subordinates that later become breeders, we translocated males and females of the same age but with different degrees of breeding experience to the islands of Aride and Cousine. Individuals were categorized as: (i) experienced breeders that had fledged young of their own in a previous year, (ii) experienced subordinates with helping but not breeding experience, and (iii) inexperienced birds that had neither helped nor bred (Komdeur, 1996b).

On the new islands, birds with helping experience paired with an experienced partner produced their first fledgling as fast as experienced breeders, and significantly faster than inexperienced birds paired with an experienced partner

ner (Fig. 1). Females with helping or breeding experience built better nests and spent more time incubating than inexperienced females. During this period no subordinates assisted any of the breeding pairs. Pairs comprising a male with breeding experience and an inexperienced female took four times longer to produce their first fledgling than pairs of a female with breeding experience and an inexperienced male (Fig. 1). This is probably a reflection of a breeding system in which only females build the nest and incubate. Once inexperienced birds had fledged young and so acquired experience, they immediately improved breeding success by producing a second fledgling in the same time as birds with either prior helping or breeding experience (Fig. 1). Environmental effects were minimized in this study because comparisons were made between breeding pairs occupying territories of equal quality.

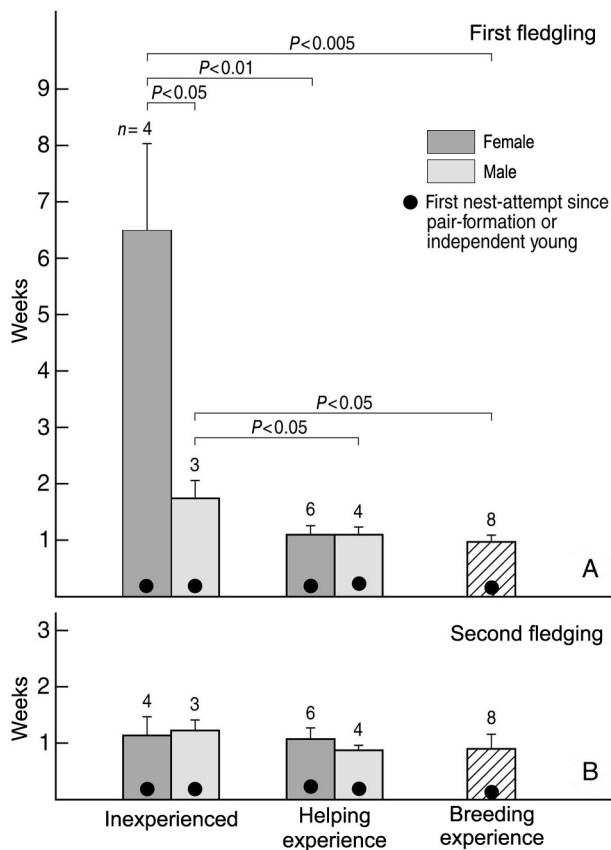


Fig. 1 Comparison of breeding efficiency in Seychelles warblers of differing breeding experience

(A) The number of weeks between pair formation and the production of the first nest and first fledgling on the islands of Aride and Cousine, plotted for male and female birds with different past experience. (B) The number of weeks between independence of first fledgling and the production of a new nest and second fledgling on the islands of Aride and Cousine, plotted for the same male and female birds as in (A) and now experienced breeders. In both cases, the birds were between 3 and 7 years of age, paired with the same experienced breeding partner, and did not receive assistance from helpers. Statistically significant comparisons determined by Mann-Whitney U tests. Only significant differences are plotted (from Komdeur, 1996a).

Another direct benefit gained by subordinate Seychelles warblers is the acquisition of parentage within the breeding group. Female subordinates often gained parentage within their own group by laying eggs in their mother's nest (44% of 43 female subordinates; Richardson et al., 2001, 2002). Subordinate males also gained direct benefits through parentage within the group (15% of 20 male subordinates), though significantly less often than females (Fisher's exact test, $P = 0.024$; Richardson et al., 2002). Female subordinates gained significantly higher direct breeding benefits (3.3x) than male subordinates, but there was no significant difference for indirect benefits between the sexes (Fig. 2; Richardson et al., 2002). Overall direct benefits were significantly higher than indirect benefits, although this difference was greater in females (Fig. 2; Richardson et al., 2002). None of the subordinate females gained reproductive success through egg dumping in other territories, and none of the male subordinates gained extra-pair fertilizations with females from other groups.

Another suggested benefit of helping is territory inheritance. This may happen in two ways. First, the act of helping in rearing younger siblings could lead to site dominance and, hence, to success when competing for a territory after the death of its owner (e.g., Zack, 1990; Koenig et al., 1992; Balshine-Earn et al., 1998). Secondly, helping can lead to increased size of the family unit and, consequently, to an increase in the size of the natal territory. Large territories may increase the likelihood that the subor-

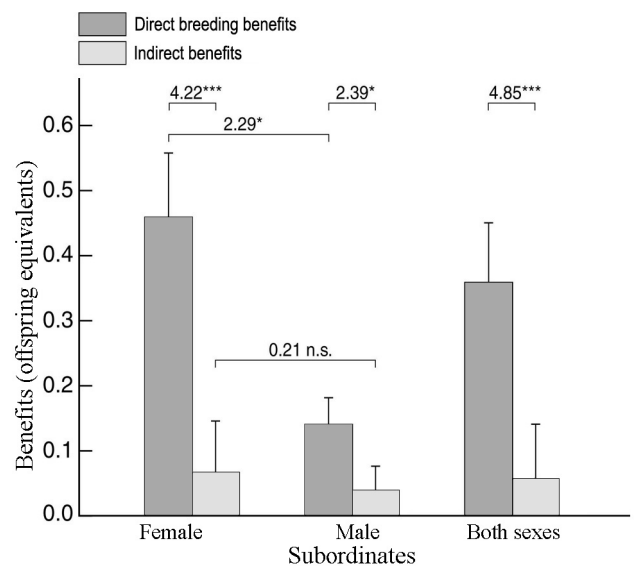


Fig. 2 Fitness benefits of cooperative breeding gained by female and male subordinates in the Seychelles warbler (1997–1999)

Statistical significance assessed by Mann-Whitney Z statistic. Both female ($n = 43$) and male ($n = 20$) subordinates gain significantly higher direct breeding benefits (open columns) compared to indirect benefits (filled columns). Direct breeding benefits are significantly higher in females than in males, but there is no significant difference between the sexes in indirect benefits. Error bars represent one standard error (from Richardson et al., 2002).

dinate will be able to 'bud off' a portion of it as a breeding territory for itself, which might additionally act as a stepping-stone for inheritance (Emlen, 1991).

In the Seychelles warbler, the added presence of male subordinates did not result in an increase in size of the natal territory, and male subordinates that helped never became budders. Because of the absence of a switch between helping and budding strategies, we were able to test whether territory inheritance is entirely the result of helping strategy: male helpers never inherited breeding vacancies after the death of the primary male ($n = 28$; Komdeur and Edelaar, 2001). Moreover, none of these helpers filled any of the nine experimentally created male breeding vacancies that contained a male helper. All male helpers eventually die without having acquired a breeding territory (Komdeur and Edelaar, 2001).

4 Discussion

Inclusive fitness benefits have been suggested as a major selective force behind the evolution of cooperative breeding (reviewed in Cockburn, 1998). One factor that complicates the study of benefits within cooperative breeding systems is the differential in benefits accrued from helping by different individuals in the group (Cockburn, 1998; Heinsohn and Legge, 1999). In systems with subordinates of both sexes, therefore, the benefits of cooperative breeding should be analyzed separately for the sexes. Such differences might in turn help to explain the skewed sex ratios of subordinates often found in cooperative species (West and Sheldon, 2002). The quantification of the direct and indirect benefits accruing to subordinates in cooperatively breeding species has only recently become possible with the advent of powerful molecular techniques that can accurately determine parentage and relatedness within the groups (Burke, 1989; Queller et al., 1993).

The Seychelles warbler is atypical among cooperative breeding birds in that females are much more likely to become subordinates than males. Recorded percentages of subordinates that are female are 88% (Komdeur, 1996a) and 68% (Richardson et al., 2002). Males typically disperse. Our results show that female subordinates gain significantly higher inclusive fitness benefits than male subordinates. Female subordinates remain on their natal territory and obtain higher inclusive reproductive success by helping closely related relatives, by co-breeding within the group, and through improved future parenting ability. Males often become subordinates on non-natal territories and so do not gain indirect reproductive success by helping. They only rarely gain direct benefits through co-breeding, and do not gain through the eventual inheritance of the territory.

The higher inclusive fitness benefits accruing to female subordinates may explain why primary females often skew the sex ratio towards producing female offspring (Komdeur et al., 1997). With female subordinates remaining on the natal territory, the primary female gains both an increase in her own productivity and also indirect benefits

associated with the breeding of subordinate females. The presence of several female subordinates in the group may, however, be a disadvantage to her, because her direct fitness may decline due to competition for food and increased risk of nest failure, mainly from egg breakage due to increased pressure from simultaneous incubation (Komdeur, 1994a). Her indirect fitness may also decline because of increased competition over local breeding vacancies between subordinate female relatives. At this stage, it is in the interests of the group that female offspring should refrain from becoming subordinates and disperse.

The balance between these forces determines whether offspring become subordinates or not. To test the role of cooperation and competition on the fitness of subordinates and their 'decision' to become a subordinate, some subordinate females should be removed from extended families. The shifts in newborn offspring would then have to be compared before and after the manipulations.

There is good evidence that inclusive fitness consequences are higher for female than male subordinates in the Seychelles warbler. The long-term inclusive fitness functions for subordinates and non-subordinates of both sexes, however, should be calculated from molecular parentage analyses and precise coefficients of genetic relatedness, in order to predict under what circumstances males and females should become subordinates.

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